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## On the Transpiration Current in Plants

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*On the Transpiration Current in Plants.*

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In a paper\* published in 1905, Professor Ewart investigates the question as to what force is required to move water through the waterways of plants at the same velocity as the transpiration current. His general conclusion is that the resistance is so great that neither are sufficient forces generated in the leaves to raise the water at the required velocity, nor is the tensile strength of water adequate to transmit these forces downwards, if such existed. In a subsequent paper he seems to have modified this latter view and quotes Berthelot as stating that air-free water may support a tension of over 200 atmospheres.†

It is needless to criticise Ewart's calculations of the resistance based on Poiseuille's formula, which he himself admits is quite inapplicable to the case, owing to the presence of cross-partitions and irregularities in the cross-sections of the tracheal tubes. It may be noticed, however, that when care was taken that discontinuities were not present in the water columns of the wood experimented upon, the flow observed approximated to the flow calculated by the formula. In an experiment on a piece of yew wood the approximation was very remarkable. The actual amount transmitted‡ through a length of 15 cm. was 4·2 c.c. per hour, while the calculated amount was 9·8 c.c. The average distance from one another of the cross-partitions in the fine tubes composing the wood is 0·25 cm. Therefore about 60 partitions must be traversed in passing through a length of 15 cm. This indicates that the resistance offered by the walls, or rather by the pits in the walls, to the passage of water is very slight.

Ewart also endeavours to find experimentally the resistance offered to the transpiration current. His first method, that of Janse and Strasburger,§ was as follows: "Leafy branches 4 to 8 feet in length were cut under water and kept in darkness for half an hour. Clean ends were then cut under water, placed in freshly filtered eosin solution, and at once exposed in the open on

\* "Ascent of Water in Trees," 'Phil. Trans.,' 1905.

† "The Resistance to Flow in Wood-vessels," 'Ann. of Botany,' vol. 19, No. 75, July, 1905.

‡ "Ascent of Water in Trees," 'Phil. Trans.,' 1905, p. 50.

§ Strasburger, 'Histologische Beiträge, 1901,' Part III, p. 778.

bright cloudless breezy June days between 10 a.m. and 1 p.m., with a shade temperature averaging  $18^{\circ}$  to  $22^{\circ}$  C. The conditions for transpiration were, therefore, optimal.

"After a timed period the stem was removed and rapidly sectionised from apex downwards until the eosin solution was visible in the wood, the length of the remaining portion of the stem giving the rate of flow during the period of observation. Portions of the same stems and also similar ones from the same plants were then subjected to varying water pressures until closely corresponding rates of flow were reached."\*

By this method, and by assuming that the velocities shown in these branches are maintained throughout the stem, Ewart obtains results which indicate that, in order to move water in the stems of plants at the velocity of the transpiration current, pressures equivalent to a head of from 6 to 33 times the height of the plant are required.

There are several reasons why this unexpected result of Ewart's must be regarded as incorrect. (1) The velocity of flow given in Ewart's experiment is probably far in excess of even the maximum velocity of the transpiration current in the intact plant. (2) The velocity cannot be assumed to be uniform throughout high trees; but may fall off from below upwards. (3) Ewart's results for the resistance to flow in stems are not in agreement with a large body of experiment to be quoted presently, but appear to be excessive.

First, with regard to the velocities in Ewart's experiment and in intact trees. In intact trees the lifting forces generated in the leaves must do work against the resistance to flow all along the path of the current, and, if the supply is inadequate from the roots, against other opposing forces in addition, and against the whole hydrostatic head. In Ewart's experiment not only are the resistance of the lower part of the conducting system, the other opposing forces and the hydrostatic head removed, but they are replaced by the atmospheric pressure acting as a *vis a tergo*, urging the water upwards. Naturally, then, a much greater velocity is attained in the latter case than when the branch is still attached to the tree.†

The subsequent wilting of the leaves of cut branches shows that clogging afterwards greatly reduces the flow; but, of course, in the experiment quoted it is only the initial stage which is recorded.

\* Ewart, *loc. cit.*, p. 24.

† It may be mentioned that Janse's method of observing the amount of transpiration by successive weighings of a severed branch is not falsified by this error, but probably gives too small an amount after transpiration has proceeded for some time. Strasburger considers that this is corrected more or less accurately by his over-estimate of the resistance (Strasburger, *loc. cit.*, p. 779).

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The assumption that the velocity in the terminal branches is as great or greater than in the trunk is also not justified. The lower leafy branches have to do work against a smaller hydrostatic head, and against a smaller resistance than the outer and upper branches, and consequently the flow will be faster through the lower parts than above. Furthermore, in many cases the effective cross-section supplying unit transpiring area is greater above than below. A good instance of this was brought under my notice by Dr. J. Joly last summer, in a young specimen of *Abies excelsa*, which had just been felled. The tree was 550 cm. high. The section at its base showed 17 year rings. The lateral branches were almost uniformly clothed with leaves, so that the length of the branches was approximately proportional to the leaf-area it supported. At 52 cm. from the apex the area of the cross-section of the wood was 0.63 sq. cm. and the sum of the length of the leafy branches above this was 170 cm. At 134 cm. from the apex the cross-section was 4.29 sq. cm. and the sum of the lengths of the leaf-bearing branches above was 1500 cm. At the higher level the cross-section of the supply conduits was 0.37 sq. cm. per 100 cm. of leafy branch, at the lower point the cross-section of the supply was 0.286 sq. cm. per 100 cm. of branch. Therefore, in the case of this tree, if all the leaves were transpiring uniformly the velocity at the lower level must be greater than above. Hence in Ewart's experiments it is quite possible that the velocity below was considerably in excess of that in the upper parts of his severed branch, and certainly without special measurements it is not legitimate to assume that the velocity throughout the length of the branch was uniform. This is equally true with regard to intact large trees.

With regard to the resistance it will be seen later on that Ewart's results are considerably too high.

The second method of determining the maximal velocity of the transpiration current employed by Ewart\* is also open to objection. It is described by him as follows: A small branch bearing a small number of leaves, while still attached to the tree, is led through a split rubber cork into an air-tight glass chamber containing a weighed quantity of calcium chloride. The gain in weight of the latter gives the amount of water transpired by the leaves in a given time. Assuming, then, that all the leaves of the tree may act like those in the closed glass chamber, the number of leaves on the whole tree will give the weight of water transpired by the tree and consequently the amount of water which passes up the tree in a given time. Then, by measuring the effective cross-section of the trunk, the velocity of the transpiration current may be estimated.

\* *Loc. cit.*, p. 56.

The objections to this method are obvious.

1. When the branch is first introduced into the desiccated chamber it will lose water more rapidly than when it was transpiring into the less dry external air. It will continue this abnormally rapid rate of transpiration until the concentration of the vacuoles of the evaporating cells reaches a steady state, depending on the freedom of supply from the water conduits and the vapour pressure in the chamber, but, until this steady state is attained the amount of water entering the calcium chloride may be largely in excess of that passing up the stem.

2. But a more serious source of error is the assumption that all the leaves of the tree can transpire at the same rate as those on the single desiccated branch, whereas the supply, which under the conditions of the experiment is available for the very actively transpiring branch, would be largely encroached upon if all the branches were under equally favourable conditions for transpiration. In fact, the single branch in the desiccated chamber and still attached to the rest of the tree, which is under normal conditions of moisture, is under conditions of supply approximating to those of a cut branch set in water and, for the same reasons, cannot be assumed to give a correct estimate of the velocity of the transpiration current throughout the whole tree.

The validity of this objection may be demonstrated experimentally by weighing the amount of water given off by a given number of leaves in a desiccated chamber, and comparing this amount with the quantity of water transpired by the same number of leaves on the same tree exposed to normal conditions of maximal transpiration.

I have made several of these experiments: A small yew-tree was removed from the flower-pot in which it had been grown, and the roots, and their surrounding soil, enclosed in a rubber bag; to prevent loss of water, except from the leaves, the opening of the bag was tied tightly round the stem. Periodic weighings gave the amount of water transpired. At the same time a branch still attached to the tree was introduced into a hermetically closed flask containing calcium chloride. The flask could be removed and weighed periodically. A rubber bag, similar to that enclosing the roots, filled with moist earth and closed, was exposed to the same conditions and weighed simultaneously, thus giving a small correction for loss through the bag. In one of these experiments the unenclosed branches supported approximately 9500 leaves, the enclosed branch 520, *i.e.*, the proportion of leaves on the single branch to those on the whole tree was 1:18. When the tree was exposed in a hot sun and brisk breeze, air temperature varying between 31° and 24° C. in the month of July, the amount transpired was 5·171 grammes

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per hour, or 0·544 gramme per 1000 leaves. The amount transpired by the desiccated branch, on the other hand, was 0·781 gramme per hour, or 1·502 grammes per 1000 leaves per hour. Hence the leaves in the desiccated chamber transpired nearly three times as much as the others under normal conditions of maximal transpiration. In this experiment the loss of water from the enclosed branch does not represent any temporary desiccation of the surface tissues, for before the weighings were made the branch had been enclosed in the flask for a day. If this initial desiccation had been included, as it was in Ewart's experiments, the difference between the amounts given off by the enclosed and unenclosed leaves would have appeared greater.

In diffuse light the difference is not so marked. The unenclosed leaves of the tree used in the last experiment in diffuse light with a temperature of 21° C. transpired 1·250 grammes per hour, or 0·130 gramme per 1000 leaves; the enclosed leaves simultaneously transpired 0·099 gramme, or 0·192 per 1000 leaves per hour. The desiccated leaves are nearly  $1\frac{1}{2}$  times as active in transpiration as those under the normal conditions.

These experiments show that it is not justifiable to assume that the rate at which water is given off by an isolated branch under conditions of abnormal desiccation is attained by all the branches when all alike are exposed to conditions most favourable to transpiration. The excess evaporation from the desiccated leaves will be greater when the bulk of the isolated branch is but a small fraction of the bulk of the whole tree; for the greater the preponderance of the latter the larger will be the supply available for the branch and consequently the less the resistance to transpiration. In Ewart's experiment, then, where the branch had only 500 leaves, while the whole tree had 9,000,000 (1:18,000), it is probable that the effectiveness of the former was much greater than that of the remaining leaves of the tree. Such an over-estimate in the amount transpired involves, according to the method, an exaggeration in the velocity of the current in the trunk.

The control of transpiration exercised by the freedom of supply may be easily observed by means of the weighing method. The amount transpired will be found to fall off as the plant exhausts the water in the soil round its roots, and to rise when the soil is again rendered moist. The following figures illustrate this fact in the case of a small yew-tree which was exposed to conditions favourable to transpiration on seven successive days. The conditions were fairly uniform, as throughout the experiment the sky was lightly overcast and a light east wind blew.

Table I.

| Transpiration per hour. | Date.   | Temperature. |
|-------------------------|---------|--------------|
| grammes.                |         | ° C.         |
| 2·65                    | July 24 | 18·5         |
| 2·14                    | " 25    | 20·5         |
| 3·25                    | " 26    | 22·0         |
| 0·87                    | " 27    | 19·5         |
| 0·97                    | " 28    | 21·5         |
| Watered—                |         |              |
| 2·23                    | " 28    | 24·0         |
| Watered—                |         |              |
| 1·59                    | " 30    | 19·0         |
| 3·05                    | " 30    | 22·5         |

The dependence of transpiration on the supply is prettily illustrated by Darwin's experiment with the horn hygroscope.\* Darwin records that when the hygroscope is applied to the leaves of a branch severed from a plant, it indicates a gradually diminishing rate of transpiration as the store of water in the branch is gradually exhausted. A diminished rate of transpiration is also indicated by the hygroscope when the supply to a branch is reduced by the application of a clamp constricting the water conduits leading to its leaves.

The diminution in the rate of transpiration in these experiments is no doubt due to a rise in the tension of the water columns supplying the evaporating cells. The tension rises in the first case as the limited water store is drawn upon, and the water surface is dragged into the cut surface of the branch. The surface-tension forces developed there then oppose the transpiration current. In the second experiment the tension is increased by the rise of the resistance brought about by the reduction of the calibre of the conduits. Further reduction of transpiration is occasioned by the closing of the stomata and by other phenomena, which are themselves direct or indirect consequences of the rise of tension in the water.

According to this view an interesting observation of Darwin's† receives a ready explanation. There is a momentary increase of transpiration in these experiments immediately after the separation of the branch and immediately after the application of the clamp. In the first case we may assume that the tension in the water supply is reduced by fracture, in the second case by the compression applied when screwing up the clamp. Transpiration obviously soon re-establishes tension, which becomes greater in both cases than it was originally.

\* Darwin, "Observations on Stomata," 'Phil. Trans.,' B, 1898, pp. 539 ff.

† Darwin, *loc. cit.*, pp. 548 ff.

In many ways, then, we see it is established that supply largely controls transpiration, and in neglecting this factor Ewart considerably exaggerated the maximal velocities of the transpiration through the stems of trees.

We come now to consider the amount of resistance experienced by the transpiration current in its passage through the water conduits.

To obtain the resistance, Ewart forced water through lengths of branches under various pressures. The pressure which gave the same velocity in the branch as that estimated by his methods for the transpiration current he took to be equivalent to the resistance experienced by the transpiration current. Ewart does not mention how he prepared the pieces, or how he cleansed the water for the experiment. The introduction of air-bubbles or of any clogging substance at the cut surface would materially exaggerate the pressure needed to obtain the observed velocity. Indeed, if the branch were transpiring actively when the experimental pieces were removed, it would not be sufficient to cut it under water; for the liquid in the branch being in tension, bubbles would be formed at the surface of the cutting knife. These bubbles would require some time to dissolve and disappear. The slimy materials exuding from the injured cells also clog the branch and raise the apparent resistance of its conduits. The comparatively high pressures with which Ewart worked would render the clogging from this source and from any impurity in the water more marked. Fig. 1 illustrates this point. The

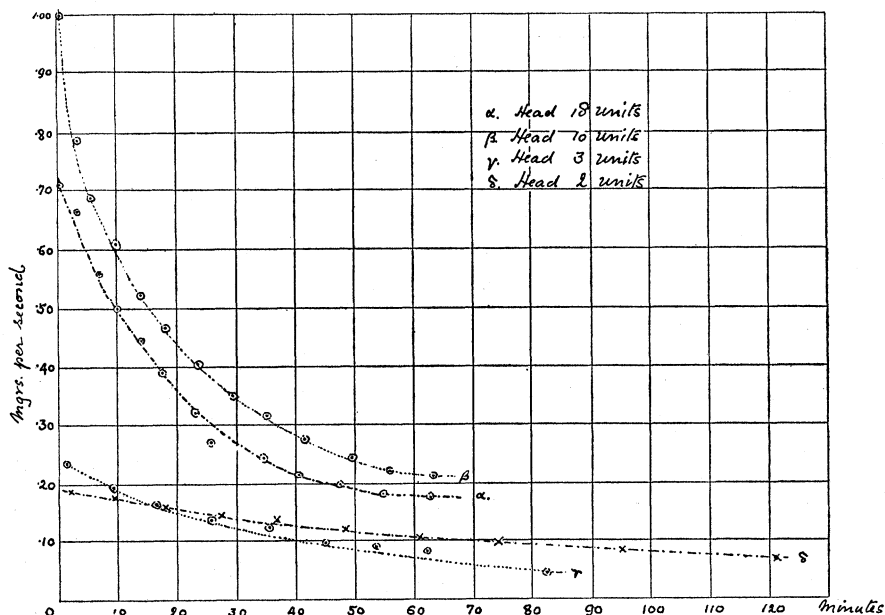


FIG. 1.

ordinates of the curves there shown indicate weights of filtered tap-water transmitted through 3 cm. of wood of *Abies pectinata* per second. The abscissæ indicate time in minutes. The curves show the diminution in the rate of transmission for each pressure, the fall-off in the amount being much more rapid for the higher pressures. From these it is seen that it is desirable (especially when using colour solutions, which from the nature of the case cannot be distilled) to employ low pressures in order to determine the resistance of the conduits apart from the surface resistance. For this reason, then, when I began to determine the resistance of the tracheidal tubes I preferred to experiment with very low pressures, assuming that the flow for higher pressures would be proportional to the head. This point was examined later.

The wood used in these experiments was that of *Taxus baccata*. The uniformity and comparative homogeneity of structure (resulting from the fact that it is composed solely of tracheids and is not penetrated by resin ducts) recommend it as far the most suitable wood for experiment, when the qualities of the water-conducting tissues are being examined. The tracheids composing the wood of *Taxus baccata* are elongate spindle-shaped chambers 1 to 5 mm. long and approximately square in cross-section. The cavity of these chambers is comparatively small. In cross-section the lumen forms about a quarter the entire area of the tracheid. The only other constituents of the wood are the cells of the medullary rays, which are radial tiers of cells 0.4 to 0.02 mm. in height. They do not materially differ in percentage from one level in the stem to another, and consequently do not introduce differences of serious magnitude. The fact, however, that they exude small amounts of slimy materials sometimes introduces difficulties. But inasmuch as there are approximately the same amount of medullary ray-cells per unit area in every cross-section, the clogging introduced in this manner is uniform and, it is to be noticed, tends to increase the apparent resistance. The presence in other woods of large medullary rays, of wood-parenchyma, of vessels of variable size, or even of resin ducts, renders them unsuitable for experiment.

Certain precautions are necessary in preparing the wood for these transmission experiments. It is best to cut away the transpiring leaves from the selected branch, and then to cut off a short length of it (say 15 to 25 cm.) under water. Five to ten centimetres are now cut from each end, and the remainder, after lying in water for at least 30 minutes, may be used directly or reduced to smaller lengths for experiment. These precautions are necessary, so that bubbles shall not be generated in the conduits. It seems possible that Ewart's high estimate of the resistance was, in part, due

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to bubbles being generated in the conduits while preparing the wood for his resistance experiments. He certainly does not mention having taken these or similar precautions in this connection, and his results are three to four times as high as those given when these precautions are taken.

When determining the velocity of flow with colour solutions, I usually worked with a head of water equal to, or less than, the length of the piece of wood experimented with. When using unit head, a fresh surface was cut with a razor on one end of a piece of a branch prepared as just described. The piece was supported vertically with the fresh surface uppermost, and a little vaseline smeared round the bark of that end. A drop of filtered concentrated eosin solution was placed on the upper surface, and as the drops formed at the lower end they were drawn away by lightly touching them with bibulous paper. As the eosin sank through the wood it was kept constantly replenished drop by drop above. After a definite time the experiment was stopped, and longitudinal cleavage of the piece of wood showed the distance travelled by the eosin solution during the time of observation at unit head. The following are the results of some of these observations :—

Table II.

| Length of piece. | Time of observation. | Distance travelled. | Velocity per hour. |
|------------------|----------------------|---------------------|--------------------|
| centimetres.     | minutes.             | centimetres.        | centimetres.       |
| 7·2              | 15·0                 | 1·7                 | 6·8                |
| 6·0              | 10·0                 | 1·2                 | 7·2                |
| 4·0              | 15·0                 | 1·7                 | 6·8                |
| 3·5              | 15·0                 | 1·8                 | 7·2                |
| 10·0             | 20·0                 | 2·2                 | 6·6                |
| 3·0              | 25·5                 | 3·0                 | 6·9                |

In the last experiment the fluid transmitted was a solution of ferrocyanide of potassium. Its presence below was detected by ferric chloride. The mean of these experiments gives a velocity of 6·9 cm. per hour under a pressure equivalent to a head of water equal in length to the experimental piece of wood.

Experiments were also made at lower pressures. For these the water-pressure was applied at the lower end of a vertical piece of wood, through a rubber tube bent into a U-shape. This tube was filled with eosin solution and the surface of the solution was raised to the desired height above the upper surface of the wood.

The mean of these observations is 8·5 cm. per hour, calculated to unit head. If we exclude the two extreme observations we get 7·6 cm. per hour

Table III.

| Length of piece. | Head.        | Distance traversed. | Time.    | Velocity per hour<br>per unit head. |
|------------------|--------------|---------------------|----------|-------------------------------------|
| centimetres.     | centimetres. | centimetres.        | minutes. | centimetres.                        |
| 8                | 2            | 0·7                 | 20       | 8·4                                 |
| 6                | 2            | 0·8                 | 20       | 7·2                                 |
| 6                | 3            | 1·8                 | 15       | 14·4                                |
| 6                | 3            | 0·9                 | 15       | 7·2                                 |
| 6                | 3            | 0·7                 | 15       | 5·6                                 |

as the velocity under a head equal in length to the stem. The last observation of the series was made on a piece of a narrow branch about 0·5 cm. in diameter, the others on pieces about 1 cm. in diameter. This difference appeared almost constantly in my experiments. The thin distal portions of the wood in almost every case offer a greater resistance to flow than the thicker parts. The high estimates of resistance are almost always obtained with the former. This fact is probably of importance in determining the total resistance in the intact plant. I have included the third observation in the table, although it diverges so markedly from the mean, because I could see no error in the experiment, and it is quite possible that a maximal result like this is the nearest to the actual flow in the uninjured tree.

The higher mean in the second series of experiments for the velocity of transmission is probably due to the fact that clogging substances are less likely to accumulate owing to the actually slower flow and to the position of the surface of application.

With care, good results may be obtained with higher pressures, if the supply is from below. In the following experiments (Table IV) the cylinder of wood was fixed in the short arm of a vertical J-tube filled with a repeatedly filtered solution of ferrocyanide of potassium. The moment of penetration through the wood, which was 3 cm. long in each case, was determined by its reaction with ferric chloride applied in a piece of bibulous paper to the upper surface of the cylinder.

The mean of the entire series gives 6·9 cm. per hour as the velocity at unit head. As all the known errors, such as the introduction of bubbles, clogging and injury of the tracheidal tubes, tend to reduce the result, it is probable that the velocity in the intact tree would be at least 7 to 8 cm. per hour under the same pressure. The occasional high results obtained indicate a still higher figure as the probable velocity.

In fig. 2 I have plotted these results. The ordinates represent the length

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traversed in one hour, while the abscissæ indicate the pressures, considering a head equal to the length of the branch as unity.

Table IV.

| Head.        | Time<br>traversing 3 cm. | Velocity per hour<br>at unit head. |
|--------------|--------------------------|------------------------------------|
| centimetres. | minutes.                 | centimetres.                       |
| 30           | 2·0                      | 9·0                                |
| 30           | 3·0                      | 6·0                                |
| 27           | 2·0                      | 10·0                               |
| 27           | 2·5                      | 8·0                                |
| 24           | 3·75                     | 6·0                                |
| 24           | 3·5                      | 6·4                                |
| 24           | 3·5                      | 6·4                                |
| 21           | 4·5                      | 5·7                                |
| 18           | 5·25                     | 5·7                                |
| 18           | 4·5                      | 6·6                                |
| 18           | 4·75                     | 6·3                                |
| 15           | 4·5                      | 8·0                                |
| 15           | 4·5                      | 8·0                                |
| 12           | 5·5                      | 8·2                                |
| 12           | 7·0                      | 6·3                                |
| 12           | 5·5                      | 8·2                                |
| 9            | 10·25                    | 5·8                                |
| 9            | 7·75                     | 7·7                                |
| 9            | 9·5                      | 6·3                                |
| 6            | 12·75                    | 7·0                                |
| 6            | 13·0                     | 6·9                                |
| 3            | 25·5                     | 7·0                                |

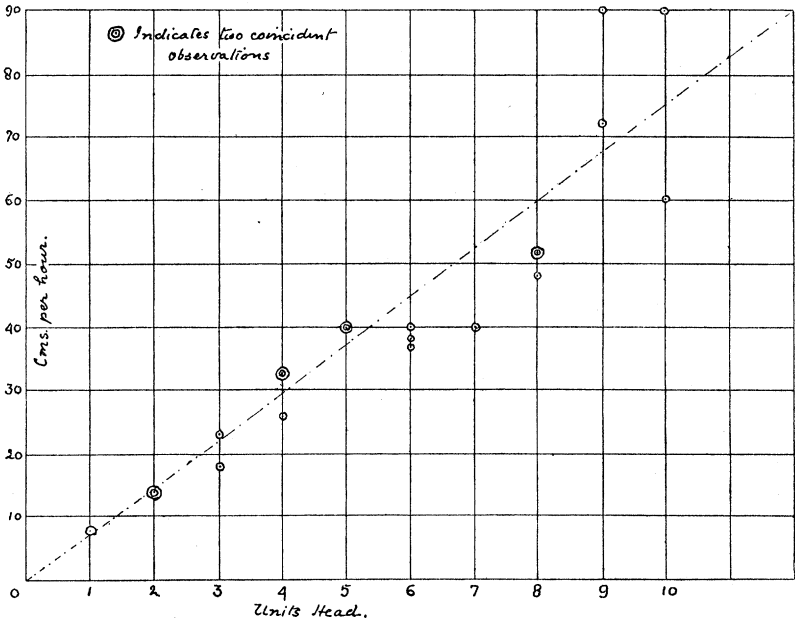


FIG. 2.

It may be noticed that the most divergent observations are those made at the higher pressures.

When we compare these results with Ewart's\* a very wide discrepancy is apparent. The results of three of his experiments allow themselves to be readily compared with my figures.

(1) He found that water travelled in a piece of yew stem, 35 cm. long, at the rate of 11.7 cm. per hour under a head of 3 metres. The head here is nearly 8.6 times the length of the transmitting wood. Assuming the velocity proportional to the pressure, at unit head the water would travel at 1.36 cm. per hour. This rate is stated to be maximal.

(2) On pp. 51 and 52 it is stated that the rate of flow in a piece of yew wood, 25 cm. long, under a head of 3 metres is 26 cm. per hour. In this experiment the head is equal to a column 12 times the length of the transmitting branch; when reduced to velocity under unit head the result is 2.17 cm. per hour.

(3) Again, on p. 55 an experiment is recorded which is suitable for comparison. A velocity of 19 cm. per hour was observed in a branch 25 cm. long under a head of 4 metres. This becomes 1.19 cm. per hour under unit head.

The mean of these three observations gives 1.57 cm. per hour as the maximal velocity of flow in the yew wood under unit head.

The results of my own numerous observations, on the other hand, made under very various conditions of pressure and by different methods, point to a velocity exceeding 7 cm. per hour with the same head.

The only explanation of this discrepancy which appears possible is that in Ewart's experiments sufficient care was not taken to prevent bubbles forming in the opened conduits and to obviate clogging at the surface. This last effect would be exaggerated in his experiments, as he worked apparently in every case at such high pressures. Reference to fig. 2 illustrates this point. There it appears that the erratic observations are those made at high pressures, although at both high and low pressures similar precautions were taken. It is in only the first of Ewart's experiments quoted above that it is mentioned that the experimental branch was cut under water. Other precautions are not mentioned.

Whatever is the cause of the discrepancy, it is certain that if Ewart had obtained my results, the difficulty of resistance, which he finds to be fatal to the cohesion-theory of the ascent of sap, would not have presented itself to him, for the velocity of 7 cm. per hour, which he demands† in the stem

\* *Loc. cit.*, p. 49.

† *Loc. cit.*, pp. 56 and 57.

of the yew, would not require a pressure equivalent to a head of 65 metres of water, as he supposes, but only to 11 metres. The recognition of the fact that unit head produces a velocity of about 7 cm. per hour invalidates his whole calculation, intended to show that to raise the sap in trees 150 metres high would require a pressure approaching 100 atmospheres. The facts of the case would be more correctly stated by saying that if the amounts transpired by isolated branches, under exceptionally favourable conditions for transpiration, were transpired by the remaining branches of the yew, and if we further assume that the velocity in the trunk is maintained out into the finest branches of high trees, then the resistance to flow in the conducting tracts would be about equal to a head of water the same height as the tree.

My results for the resistance, which were obtained as described above by directly measuring the velocity of flow under a given head, were fully confirmed by other experiments in which the amount transmitted under a given head was observed. An estimate of the cross-section effective in transmitting the current then gives the velocity.

A piece of a branch of *Taxus baccata*, 4 cm. long and having a woody cylinder 1.35 cm. in diameter, was placed with its long axis vertical. Water was supplied at its upper surface just as quickly as it percolated through the wood, so that the upper surface of the wood was continually wet, but the water was never appreciably piled upon it. The amount of water transmitted in this manner under unit head was 1.356 gramme per hour. In order to find the effective cross-section, after this observation was made, a solution of eosin was supplied under similar conditions. By this means the transmitting portions were coloured, and the area of their cross-section easily estimated. A mean of three such estimations gave the effective cross-section as 0.7 sq. cm. From this it appears that under unit head 1.93 grammes is transmitted per square centimetre per hour. Assuming with Ewart that the lumina occupy about 0.25 of the cross-section, the velocity to secure this rate must have been 7.5 cm. per hour. This agrees well with the results obtained with the other method.

In order to determine the amount of flow without danger from the error of clogging at the surface of supply, the flow was measured in a lateral branch springing from a stout stem. Water under pressure was supplied at the two cut ends of the stem. With this arrangement, owing to the relatively large surfaces of supply, the clogging taking place at these does not encroach upon the amount necessary for the supply of the small lateral branch for several hours, and consequently the rate of transmission in the lateral branch remains constant for several hours. To quote one of these experiments: A piece of yew stem 7.3 cm. long, having a straight lateral

branch at its middle length, was selected. The diameter of the stem was 0.85 cm. and 1.05 cm. at each end respectively. Its wood was also laid bare by an oval scar where another lateral branch was removed. This scar was 1.3 cm. by 1.1 cm. The small lateral branch was cut to a length of 10.5 cm., and its wood had a diameter of 0.47 cm. Not more than a quarter of its cross-section was in a state suitable for transmitting water—the greater part being occupied by blackened duramen. This lateral branch was fixed water-tight in a rubber bung in an orifice in the bottom of a tank in such a manner that the cut end of the lateral branch projected from the tank, while the supporting stem was immersed in the water in the tank. With the head of 30 cm. 0.300 gramme were transmitted per hour. The transmitting cross-section was about 0.043 sq. cm. One-quarter of this area would be lumen: therefore the velocity of flow must have been 27.2 cm. per hour. If we reduce this to unit head the velocity becomes about equal to 9.4 cm. per hour, which again falls within the limits of the results obtained by the previous method.

Throughout this discussion it has been assumed that the velocity is proportional to the pressure. This is usually done. Fig. 3 shows that this is certainly approximately true for pressures up to 16 units head. On fig. 3 are plotted the results of many experiments, the object of which was to determine if the amount transmitted in a given time is proportional to the pressure, as the former assumption would involve. The utmost care was taken to obtain clean water to supply to the wood and to free the latter from clogging material as much as possible. The water used was carefully distilled, the vessels and tubes of supply were repeatedly washed with distilled water before using, and the surface of the wood freshly cut and rinsed with distilled water immediately before the experiment began. The woody cylinder was 3 cm. long. It was supported horizontally, and a tongue of bibulous paper was applied to the outer surface of the wood and hung down vertically into a little phial which received the drops of transmitted water. The time required for five drops to fall from the tongue was noted by means of a stop-watch, and the weight of these five drops determined by weighing the phial. The mean of three such observations is given below (Table V) for each pressure.

These results confirm the received view that the amount transmitted varies directly with the pressure. The slight bending over of the line joining the observations at the high pressures is amply explained by the gradual clogging which takes place despite all precautions; for the experiments giving these results were made with the same piece of wood after those at lower pressures had been carried out.

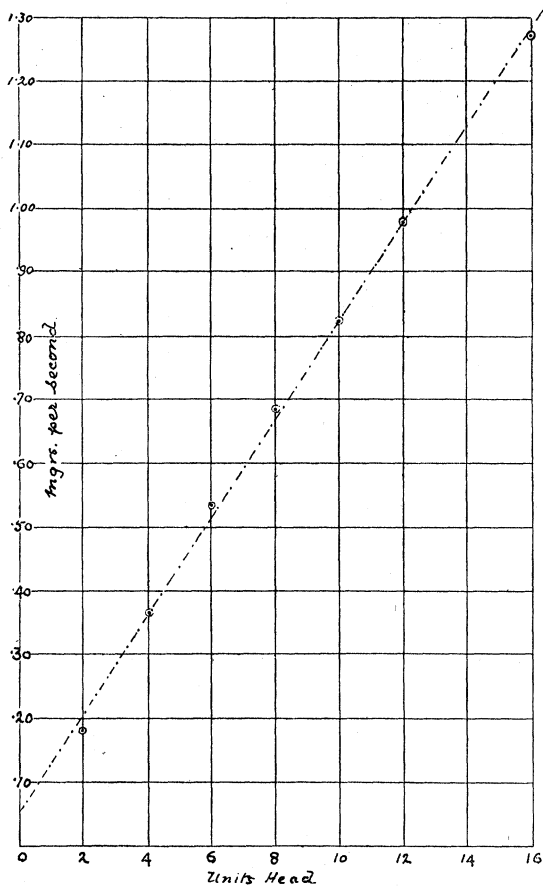


FIG. 3.

Table V.

| Head.        | Milligrammes transmitted. | Time.    | Milligrammes per second. |
|--------------|---------------------------|----------|--------------------------|
| centimetres. |                           | seconds. |                          |
| 6            | 44.0                      | 246      | 0.182                    |
| 12           | 50.0                      | 137      | 0.365                    |
| 18           | 53.0                      | 99       | 0.535                    |
| 24           | 50.0                      | 73       | 0.685                    |
| 30           | 52.0                      | 63       | 0.825                    |
| 36           | 58.0                      | 60       | 0.966                    |
| 48           | 59.5                      | 47       | 1.266                    |

The proportionality of head to flow may be indirectly investigated in another manner. A straight branch fixed in a horizontal position is connected to a large vessel of distilled water. Precautions are taken to clean the connections

and the freshly cut inner end of the branch. A tongue of bibulous paper is applied to the outer end to draw off the transmitted water. The head once adjusted is kept constant; but after each determination the branch is shortened. Fig. 4 records such a series of experiments. The head throughout these was 100 cm. The initial length was 25 cm. At that length the flow was 1.18 mg. per second. Five centimetres were then cut off the outer end and the flow rose to 1.66 mg. per second. A shortening to 15 cm. increased the flow to 2.33 mg. When the branch was 10 cm. and 5 cm. long, the flow was 3.79 mg. and 6.70 mg. respectively. The curve plotted in fig. 4

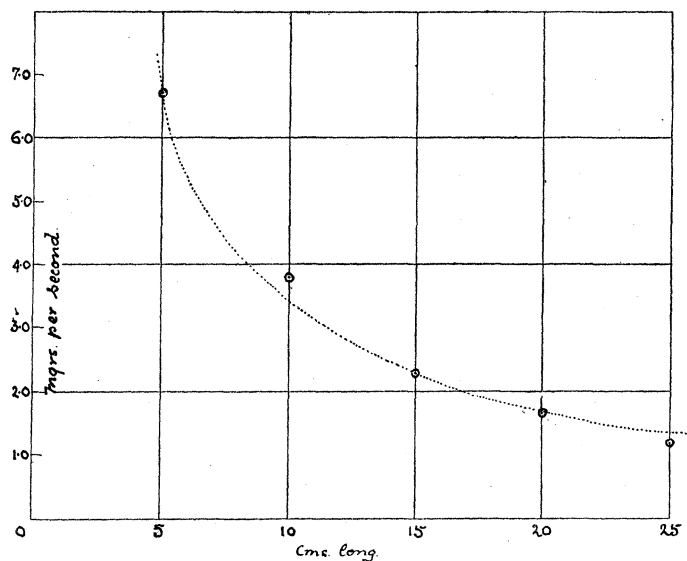


FIG. 4.

is a rectangular hyperbola in which  $M = K/l$ ;  $M$  being the number of milligrammes transmitted per second,  $l$  = length of wood, and  $K$  = average value of the product  $Ml$  observed. The observations, it may be seen, approximate fairly closely to this curve. When the weights of transmitted water are plotted against units head the curve shown in fig. 5 is obtained. Here the proportionality of flow to head, or, rather, the inverse proportionality of flow to length, is immediately apparent. Up to 10 units the curve is almost a straight line. The bending over which occurs after that point is to be attributed to the clogging, which is practically unavoidable when the flow is rapid.

In conclusion, it seems to me that Ewart's objections to the cohesion-theory, based as they are on an excessive estimate of the velocity of the transpiration current and of the resistance to this current in the conduits,

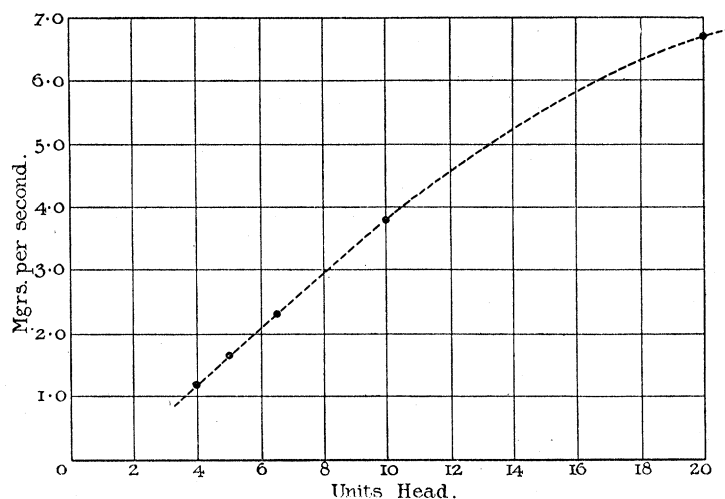


FIG. 5.

fall to the ground. With regard to the soundness of the cohesion-theory itself, apart from the weighty evidence which has elsewhere been adduced in its favour,\* the fact that other theories, both old and new, have to assume properties for the water-ways of plants which are either in the highest degree improbable according to received scientific views, or are even directly negated by experiment, seems to support the theory by a process of exclusion.

\* Dixon and Joly, "Ascent of Sap," 'Phil. Trans.,' B, 1895; Dixon, "Physics of the Transpiration Current," 'Notes from the Botanical School, Trinity College, Dublin,' May, 1897.